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Clonal alien plants in the mountains spread upward more extensively and faster than non-clonal

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Abstract

Alien species are colonizing mountain ecosystems and increasing their elevation ranges in response to ongoing climate change and anthropogenic disturbances, posing increasing threats to native species. However, how quickly alien species spread upward and what drives their invasion remains insufficiently understood. Here, using 26,952 occurrence records of 58 alien plant species collected over two centuries in the Czech Republic, we explored the elevation range and invasion speed of each alien species and the underlying factors driving these variables. We collected species traits relevant for invasion (e.g., clonality, flowering time, life span, invasion status, height, mycorrhizal type, native range, naturalized range, monoploid genome size, and Ellenberg-type indicator values for light, temperature, and nitrogen), human-associated factors (e.g., introduction pathways and the sum of economic use types), and minimum residence time. We explored the relationships between these factors and species' elevation range and invasion speed using phylogenetic regressions. Our results showed that 58 alien species have been expanding upward along mountain elevations in the Czech Republic over the past two centuries. A stronger effect of species' traits than human-associated factors has been revealed, e.g., clonality was a key trait supporting the invasion of alien species into the mountains, while human-associated factors showed no effect. Our findings highlight that the characteristics associated with rapid reproduction and spread are crucial for alien species' invasion into montane regions. Identifying key drivers of this process is important for predicting the spatiotemporal dynamics of alien species in high-altitude ecosystems and thus employing apposite measures to reduce the threat to native plant species.

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Keywords
Alien plant species, clonal trait, elevation range, human activities, invasion speed, mountain invasions

Introduction

Mountains are of crucial importance for biodiversity conservation (Rangel et al. 2018; Rahbek et al. 2019). Conventionally, these regions were considered to be relatively unharmed by alien species (McDougall et al. 2011; Alexander et al. 2016). However, with intensifying climate change and human pressure, alien species are now colonizing mountains and increasing their elevation range upward, posing a significant threat to native species (Pauchard et al. 2009; McDougall et al. 2011; Pyšek et al. 2011; Alexander et al. 2016; Dainese et al. 2017; Koide et al. 2017). Consequently, a comprehensive understanding of the increasing trends in alien species distribution and the speed at which alien species are establishing at different elevations becomes imperative for effective conservation strategies in mountain regions (Iseli et al. 2023).

In mountainous areas, the influx of alien species typically commences at lower elevations before gradually spreading upward over time (Alexander et al. 2011; Pyšek et al. 2011; Marini et al. 2013). The directional ecological filtering hypothesis, a phenomenon of a decline in alien species richness with increasing elevation due to a progressive species loss, is often invoked to elucidate the distribution of alien flora along altitudinal gradients worldwide (Alexander et al. 2011). In addition, the upward expansion of alien species is associated with minimum residence time (Pyšek et al. 2011). Recent investigations have underscored its significant role in shaping the potential elevation range of alien species (Pyšek et al. 2009a, 2011, 2015; Alexander et al. 2011), because longer residence time allows for more extensive dispersal or can result in genetic adaptation (Becker et al. 2005; Haider et al. 2010; Pyšek et al. 2011).

In addition to the minimum residence time, various characteristics of alien species, e.g., introduction pathways (Alexander et al. 2011), economic utility (Balestri et al. 2018, van Kleunen et al. 2020), proximity to road networks (Dainese et al. 2017; Skálová et al. 2017), as well as their inherent traits (e.g., dispersal abilities, climatic adaptability, and genetic adaptation) (Dietz and Edwards 2006; Alexander 2010) have been recognized as key drivers of species' range expansion. Theoretically, deliberately introduced and economically valuable plants (Pergl et al. 2017; Balestri et al. 2018; van Kleunen et al. 2018) often exhibit larger propagule pressure in terms of both propagule quantity and frequency of introduction events, consequently enhancing the likelihood of successful establishment. In addition, species with rapid growth, short generations, and strong competitive ability are also more likely to become successful invaders (van Kleunen et al. 2010). For instance, plant height was found to be positively related to species' range and probability of invasion (Pyšek et al. 2009a, 2015; Divíšek et al. 2018); optimal flowering time, functioning as a reproductive trait, ensures seed fertility

(Celesti-Grapow et al. 2003; Godoy et al. 2009), and species with earlier flowering can avoid competition and expedite the life cycle, leading to prompt reproduction. On a macroecological scale, clonality was reported to play a positive role in the invasion success and distribution of alien species (Pyšek 1997; Liu et al. 2006; Wang et al. 2024) and species primarily engaging in asexual reproduction also tend to exhibit broader ranges (Cosendai et al. 2013). Moreover, studies have shed light on how the geographic expansion of alien plants benefits from the presence of mycorrhizal associations, which form specialized structures aiding vegetative dispersal (Menzel et al. 2017; Correia et al. 2018; Pyšek et al. 2019).

Karyological characteristics were recently suggested as an important trait underpinning plant invasion success, and species with small genomes proved to be at an advantage in the process of alien plants' naturalization (Kubešová et al. 2010; Suda et al. 2015; Lopes et al. 2021; Pyšek et al. 2023) as the "large genome constraints" proposed (Knight et al. 2005). However, the advantage of possessing a small genome does not translate into the more advanced stage of the invasion process characterized by the rapid spread; here, the opposite is true as species with relatively large genomes are more likely to be successful invaders (Lopes et al. 2021; Carta et al. 2022; Pyšek et al. 2023).

While the magnitude of a species' native range significantly influences its preadaptation to the introduced environment, and a broader native range generally fosters greater readiness for the establishment and thriving within the novel environment (Pyšek et al. 2015; Guo et al. 2019; Fristoe et al. 2023), the inclusion of species-specific environmental preferences, e.g., optimal values or ranges for existence, development, growth, and reproduction, can offer a more nuanced understanding of species' spatial expansion patterns, particularly along environmental gradients like elevation (Di Biase et al. 2023). Despite these insights, scant knowledge exists regarding the key driving forces behind changes in the elevation range or vertical spread of alien plants (Dainese et al. 2017; Auld et al. 2022), especially when considering the relatively low propagule pressure at high elevations (Alexander et al. 2011).

In this study, we aim to estimate the speed at which alien species increase their elevation range and identify the drivers that underlie such invasions. Specifically, we calculated the elevation range and invasion speed of 58 alien species for which such data exist in the regional dataset for the Czech Republic. We also used various characteristics of these plants, including both species' inherent traits (e.g., clonality, flowering time, monoploid genome size, and Ellenberg-type indicator values reflecting ecological demands) and human-associated factors (e.g., introduction pathways and economic use types). We then used phylogenetic regressions to identify the key drivers of elevation range and invasion speed. We hypothesized that: 1) alien species are expanding upward along mountain elevations in the Czech Republic; 2) both species' inherent traits and human-associated factors contribute to the upward of alien species, and play distinct roles in determining the elevational range (and changes) and invasion speed.

Materials and methods

Species distribution records

Species data were obtained from an existing dataset (Williamson et al. 2005; Pyšek et al. 2011), originally including 65 alien species introduced to the Czech Republic after 1500 AD. The dataset compiled the elevation of alien species in the mountains since the year 1738, with 28,288 occurrence records in total. Based on this data, we calculated each species' elevation range ($Elevation_{max} - Elevation_{min}$) (m), invasion speed ($(Elevation_{max} - Elevation_{year\_of\_1st\_record})/ (year_{max\_elevation} - year_{1st\_record})$) (m/year), and the minimum residence time ($2022 - year_{1st\_record}$).

From the complete dataset, we removed abnormal values of invasion speed, e.g., values for species with no elevation record in the year of first introduction; values for species for which there was less than 40 years since their first introduction to the maximum elevation year, due to the possibility of inadequate sampling; and negative values. We used the '*WorldFlora*' R package (Kindt 2020) to standardize all taxon names before matching species trait data further.

Species traits

We obtained data on the clonality (modular species with potential vegetative reproduction or unitary species without this potential), flowering time (as the first month of flowering), life span (annual, perennial, or both), and invasion status (casual, naturalized, invasive) of the 58 alien species from existing datasets (Williamson et al. 2005; Pyšek et al. 2022). The categories of invasion status are based on a well-defined framework (Blackburn et al. 2011): alien species that do not form self-sustaining populations in the introduced regions are casuals; alien species that form self-sustaining populations for several life cycles in the introduced region without human intervention are naturalized; and alien species that can maintain self-replacing populations at considerable distances from their parents and/or sites of introduction, producing reproductive offspring and having the potential to spread over long distances are invasive.

The height of each species was extracted from the LEDA database (https://uol.de/en/landeco/research/leda) (Kleyer et al. 2008) using an average method. We then compiled Ellenberg-type indicator values for light, temperature, and nitrogen for each species, which are expert-based rankings of plant species according to their ecological optima on main environmental gradients (recently updated and harmonized: Tichý et al. 2022). Smaller Ellenberg-type indicator values represent species that are better adapted to the lower levels of a given factor. Mycorrhizal types were obtained from the FungalRoot v.2.0 database (Soudzilovskaia et al. 2022), divided into arbuscular mycorrhizal (AM) and non-mycorrhizal (NM) plant species.

Native range data for alien species were extracted from the POWO (Plants of the World Online; https://powo.science.kew.org/) database, and naturalized range

data were obtained from the GloNAF (Global Naturalized Alien Flora) database (van Kleunen et al. 2015, 2019; Pyšek et al. 2017). These two range-related data were expressed as the number of the Taxonomic Database Working Group (TDWG) level 3 regions (level 3 corresponds to "Botanical Countries") in which species are recorded as native or naturalized, respectively (Brummitt, 2001). Monoploid genome sizes (i.e., DNA content in a single chromosome set, *sensu* Greilhuber et al. (2005)) for the species were filtered from the Plant DNA C-values (https://cvalues.science.kew.org/) (Pellicer and Leitch 2020).

Human-associated factors

Information on the introduction pathway (deliberate or accidental introduction) of each alien species to the Czech Republic was taken from Pyšek et al. (2012). Then, we collated the economic use data of each species from the WCUP (World Checklist of Useful Plant Species; Diazgranados et al. 2020). The WCUP list provides information on 10 distinct economic uses, such as medicines and materials. We calculated the overall sum of economic use types for each species and set the economic use of species not included in the list as zero.

Phylogenetic tree

To consider potential phylogenetic relatedness across the species, a phylogenetic tree was created for the 58 species using the '*V.PhyloMaker*' package based on the default setting (Jin and Qian 2019). This phylogenetic tree was used to impute the missing traits values and subsequent statistical analyses.

Imputation of missing trait values

Given the presence of missing data for certain species, we undertook gap-filling processes as follows. For the 20 species lacking monoploid genome size, imputation was carried out utilizing the full dataset of 12,273 species (Pellicer and Leitch 2020) via the R package '*Rphylopars*' (Goolsby et al. 2017). The 11 species lacking Ellenberg-type indicator values and four species without mycorrhizal types were supplemented by data from the same genus, given the strong phylogenetic conservatism for these indicators (Prinzing et al. 2001). Finally, a list of 58 alien plant species with 26,952 occurrence records and complete values was obtained, and 45 species for the invasion speed.

Statistical analyses

All data analyses and visualizations were performed in R v4.2.1 (R Core Team 2023). First, Pearson correlation analysis was performed with all the continuous variables (i.e., invasion speed, flowering time, plant height, Ellenberg indicator values for light,

temperature and nutrients, native range size, naturalized range size, the sum of economic uses, monoploid genome size, and minimum residence time), which showed no strong collinearity among the variables (Appendix 1: Fig. A1; $r < 0.7$). Plant height, native range size, naturalized range size, and monoploid genome size were log-transformed to approximate normal distribution. To examine whether the elevation range and invasion speed varied across the categories of clonality, invasion status, life span, mycorrhizal types, or introduction pathways, phylogenetic ANOVA models were used with function '*phylANOVA*' in R package '*phytools*' (Garland et al. 1993; Revell 2012). Phylogeny is considered in the analysis because species may not represent statistically independent data points, thus avoiding unreliable model estimates (Garland et al. 1993). *P*-values were determined by Brownian motion model simulation phylogeny, which was run 10,000 times. To explore the combined effects of continuous variables on elevation range and invasion speed of alien species, phylogenetic multiple linear regression models were employed (Si et al. 2022). Models were run separately for clonal and non-clonal species and the variables selection was conducted using the '*phylostep*' function in the '*Phylolm*' package (Tung Ho and Ané 2014). All numerical variables were standardized to gain standardized coefficients so that comparisons between and within models could be possible (Schielzeth 2010). Finally, according to the results of the '*phylostep*', several predictors were identified as key drivers for both clonal and non-clonal alien species, which were used in regressions on data of clonal species, non-clonal species, and all species.

Results

The elevation ranges of the 58 alien species varied from 132 m to 1095 m (Fig. 1). *Heracleum mantegazzianum* had the largest elevation range (1095 m) and the highest upper elevation limit, peaking at 1294 m a.s.l. In contrast, *Panicum dichotomiflorum* had the smallest elevation range (132 m) and the lowest upper elevation limit with a peak of 271 m a.s.l. As for the elevational invasion speed of the 45 alien plants analyzed, it was fastest for *Mimulus guttatus* with 8.4 m/year, whereas for *Ambrosia artemisiifolia* it was the slowest (0.5 m/year) (Fig. 1). Generally, species with large elevation ranges also had high invasion speeds (Appendix 1: Fig. A1).

Both elevation range and invasion speed differed with regard to clonality (Fig. 2a, c; $P < 0.01$). Specifically, clonal species had significantly larger elevation ranges (average values of clonal vs. non-clonal species = 709 m vs. 500 m, $P = 0.001$) and higher invasion speeds (5.4 vs. 3.7 m/year, $P = 0.004$) than non-clonal species (Fig. 2a, c). Casual species had the smallest elevation ranges compared to both naturalized and invasive species (357 m, 613 m, and 688 m on average, respectively, $P < 0.05$), which were not significantly different from each other (Fig. 2b; $P > 0.05$). Likewise, no significant differences were observed in invasion speed among the three categories of invasion status (Fig. 2d). Moreover, neither elevation range nor invasion speed

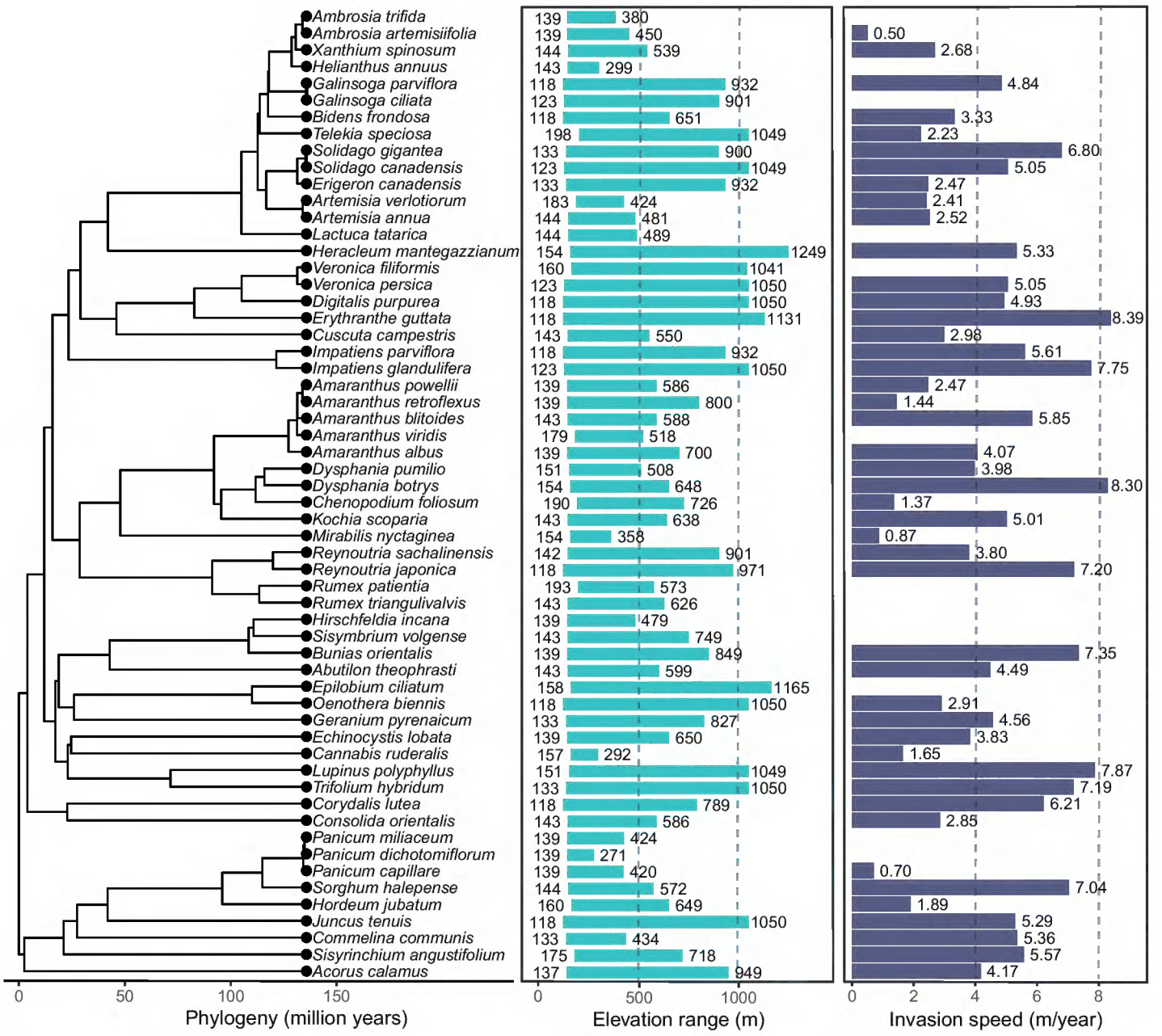

Figure 1. Phylogenetic tree of the examined 58 alien plant species in the Czech Republic, with their elevation ranges (m) and invasion speeds (available for 45 species, m/year) aligned.

differed among different life spans, mycorrhizal types, and introduction pathways (Appendix 1: Fig. A2).

Phylogenetic regressions revealed different factors driving the elevation range and invasion speed for clonal and non-clonal species (Figs 3, 4). Specifically, for both clonal and non-clonal species, species' invasion speed and minimum residence time showed positive effects on elevation range, whereas Ellenberg indicator values for temperature and the time of flowering showed negative effects, with species demanding a higher temperature and those that start flowering early having small elevation ranges (Figs 3a, 4). As for elevational invasion speed, native range size was the only predictor showing a negative effect on the invasion speed of non-clonal species (Fig. 3b). For clonal species, the invasion speed was negatively associated with Ellenberg indicator values for temperature, and with minimum residence time, and positively to naturalized range size (Fig. 3b).

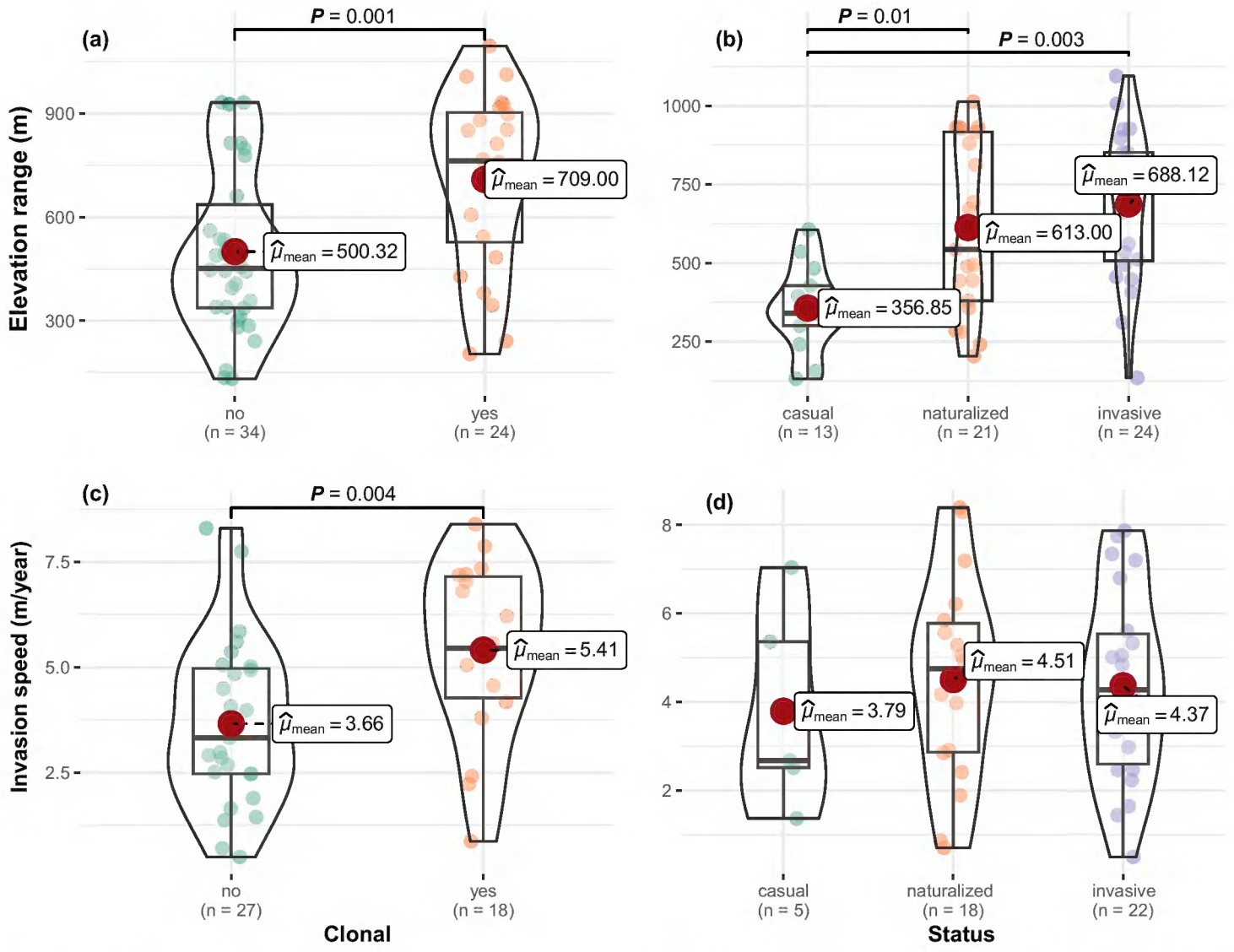

Figure 2. Violin plots showing the elevation ranges and invasion speeds of the examined alien species, categorized based on their clonality and invasion status. Note that the invasion speed was only available for 45 species. For the boxplots inside each violin plot, the horizontal line, red dot, and box, respectively, represent the median, the mean, and the interquartile range. *P*-values were obtained from phylogenetic ANOVAs and showed in the upper part of the violin plot if significant ($P < 0.05$).

Discussion

Using more than 26,000 historical occurrence records of 58 alien plant species introduced to the Czech Republic after 1738, we found a substantial upward shift along the elevations for the majority of the species analyzed (Fig. 1). The speed of spread to the higher elevation ranged from 0.5 to 8.4 m/year, with species capable of reaching the highest elevation also exhibiting the fastest invasion speed (Fig. 1). Our findings are in line with a recent study showing that alien plant species were expanding their upper elevation limits in 10 out of the 11 surveyed mountains across five continents (Iseli et al. 2023). However, no upward expansion of alien plants was observed in several regional studies, e.g., 67% of naturalized invasive plant species in California showed no mean elevation shift over the past century (Wolf et al. 2016). On the island of Hawaii, both the upper and lower elevation limit of 20 alien species are moving up, but elevation ranges did not change significantly over 40 years (Koide et al. 2017). In Europe, 10% of alien species exhibited a potential downslope shift (Dainese et al. 2017). Although these contrasting findings may be due to different climates and land-use

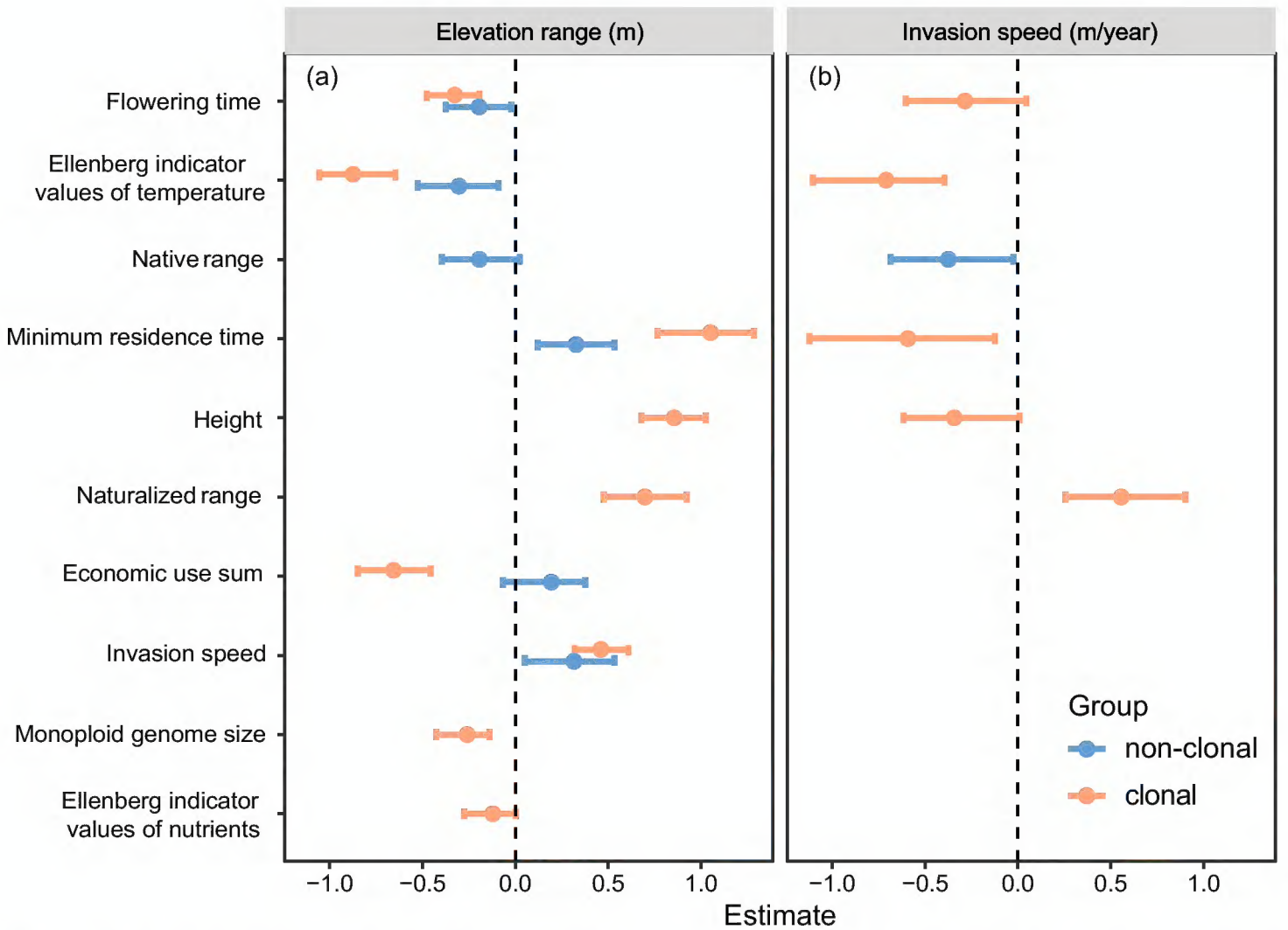

Figure 3. Standardized estimates and associated 95% confidence intervals obtained from phylogenetic regressions for each of the elevation range and invasion speed models. Models were run separately for clonal (orange) and non-clonal (blue) species and the variables were selected via the '*phylostep*' function in the R package *'Phylolm'*. In particular, we added invasion speed as an additional variable for the elevation range. Confidence intervals that do not cross the zero line indicate that the estimates are significant ($P < 0.05$).

history between the studying areas (Iseli et al. 2023), an understanding of the driving factors underlying the range expansions along elevation is emerging.

Among the various factors tested in this study, alien species with clonal reproduction exhibited not only significantly broader elevation ranges but also faster upward expansion compared to their non-clonal counterparts (Fig. 2a, c). Such a result is in line with previous studies showing that species primarily reproducing through asexual means tend to have broader distribution ranges (Cosendai et al. 2013). Besides, alien clonal species were found to have better growth performance than native clonal species, highlighting the pivotal role of clonality in promoting plant invasion (Pyšek 1997; Liu et al. 2019; Wang et al. 2019). Here, we also found that among clonal alien species, the taller ones exhibited a tendency for broader elevation ranges, and those with larger naturalized ranges had greater elevation ranges and speeds (Fig. 3a, b).

For other traits tested with regard to the elevation expansion of alien species, we observed a negative association between monoploid genome size and elevation range for clonal aliens (Fig. 3a). This can be explained by the "large genome constraints" hypothesis, stating that large genome acts as a constraint in extreme

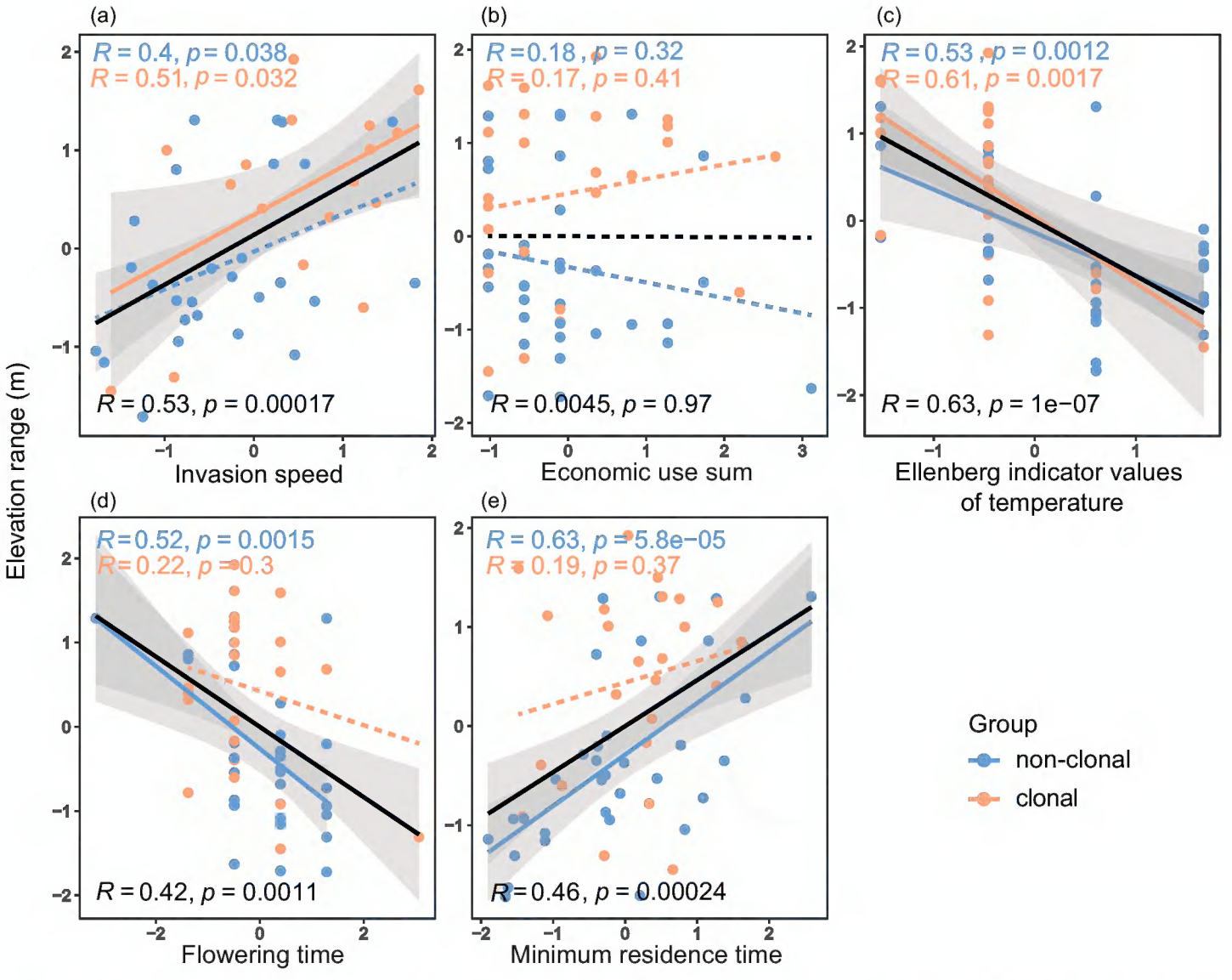
(a)
R = 0.4, p = 0.038
R = 0.51, p = 0.032
R = 0.53, p = 0.00017
Invasion speed
(b)
R = 0.18, p = 0.32
R = 0.17, p = 0.41
R = 0.0045, p = 0.97
Economic use sum
(c)
R = 0.53, p = 0.0012
R = 0.61, p = 0.0017
R = 0.63, p = 1e−07
Ellenberg indicator values of temperature
(d)
R = 0.52, p = 0.0015
R = 0.22, p = 0.3
R = 0.42, p = 0.0011
Flowering time
(e)
R = 0.63, p = 5.8e−05
R = 0.19, p = 0.37
R = 0.46, p = 0.00024
Minimum residence time
Elevation range (m)
Group
non-clonal
clonal

Figure 4. Relationships between elevation ranges and important variables identified from phylogenetic regressions (See Fig. 3 for details; data were log-transformed). Blue, orange, and black lines represent regression lines with non-clonal, clonal, and all species, respectively. The dashed lines represent non-significant relations. Grey shading represents 95% confidence intervals.

and inhospitable conditions (Knight et al. 2005), which can be applied to alien species' establishment in higher elevation. The invasion speed was strongly associated with clonality, and for non-clonal alien species, only their native range size was negatively related to their upward spread (Fig. 3b). Although native range size was closely related to the fitness of alien species in the introduced areas (Pyšek et al. 2015; Guo et al. 2019; Fristoe et al. 2023), the inherent characteristics and interactions with local native species may be more important in determining the invasion speed of alien species. In essence, these results highlight the multifaceted interplay between clonality, height, genetic characteristics, and climate niche, revealing the intricate dynamics that contribute to the upward expansion and invasiveness of clonal alien plants.

In addition, our study identified the minimum residence time, flowering time, and demands for temperature as key factors driving the elevation range of alien species in the Czech Republic, regardless of their clonality status (Fig. 3a). Such results indicate that alien plants which are more likely to have a wider elevation range are those that

start flowering earlier, arrive earlier and have a reduced dependence on temperature conditions. These characteristics are also commonly observed in alpine plants (Alexander et al. 2016; Inouye 2020; Wang et al. 2020) and contribute to the expansion of their ecological range.

It is gradually recognized that the position on the introduction-naturalization-invasion continuum is a good indicator of species' minimum residence time (Pyšek et al. 2009b; Moodley et al. 2013), thus aligning with the minimum residence time results: the elevation ranges of the 58 alien species increased along the introduction-naturalization-invasion continuum (Fig. 2b). While the same trend along the invasion continuum was not obtained for the invasion speed of alien species, a negative relationship was uncovered between the minimum residence time and the invasion speed for clonal species. The suitable ecological niche of the species may be responsible for this phenomenon, i.e., alien species with longer minimum residence time may have already occupied the most suitable habitats and, therefore, have slower invasion speeds. On the other hand, the relatively limited availability of valid invasion speed data for the initial two stages, in comparison to the third stage, might have introduced a degree of compromise to the statistical analysis. This potential data limitation could lead to the nuanced results observed in this context.

For human-associated factors, we hypothesized that the economic use of alien plants will positively correlate with their elevation ranges, in keeping with the well-established assertions of earlier research, which underline the significance of economic use in determining the success of alien plant species within introduced ranges (Guo et al. 2019, van Kleunen et al. 2020). However, our results did not match the second hypothesis we proposed. This may be due to nearly a quarter of alien species not having economic use data. Similarly, the results for the introduction pathway had no significant effect on driving alien species expansion along elevation (Appendix 1: Fig. A2). This could be caused by other human-related factors which could have greater predictability, such as distance to roads. Proximity to roads proved to be a key driver of the observed rapid upward spread of alien species (Dainese et al. 2017).

Although we considered several factors related to species' expansion along the elevation gradient, several important variables, such as climate and soil properties, were missing from the analysis. It appears necessary to include these variables in future studies to gain a more comprehensive understanding. Interactions between alien and native species are equally important to become a subject of future studies, with the potential to provide valuable insights into the mechanisms underlying the establishment and persistence of alien species in alpine habitats.

In summary, our results showed that 58 alien species have been expanding upward along mountain elevations in the Czech Republic over the past two centuries. Alien species can reach the highest elevations and exhibit the widest range of elevations, providing further support for the hypothesis of directional ecological filtering. In particular, our study explored how species traits and human-associated factors influence the elevation range and invasion speed of alien species towards mountains. We found distinct roles of species characteristics and human-associated factors in shaping species'

elevational expansion, e.g., compared with non-clonal alien species, clonal alien species had a wider elevation range and faster invasion speed, while human-associated factors had no effect. Our results emphasized that rapid reproduction and spread are crucial for alien species' expansion in mountainous regions and are further facilitated by long residence time. Identifying key drivers of the distribution and spread of alien species in mountain areas and further developing a more complete understanding of how traits, human factors, and climate interact is critical. By analyzing complex temporal patterns and trends in the distribution of alien species, we can better grasp their dynamics and potential impacts on local ecosystems given the dynamic climate change worldwide.

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Appendix I

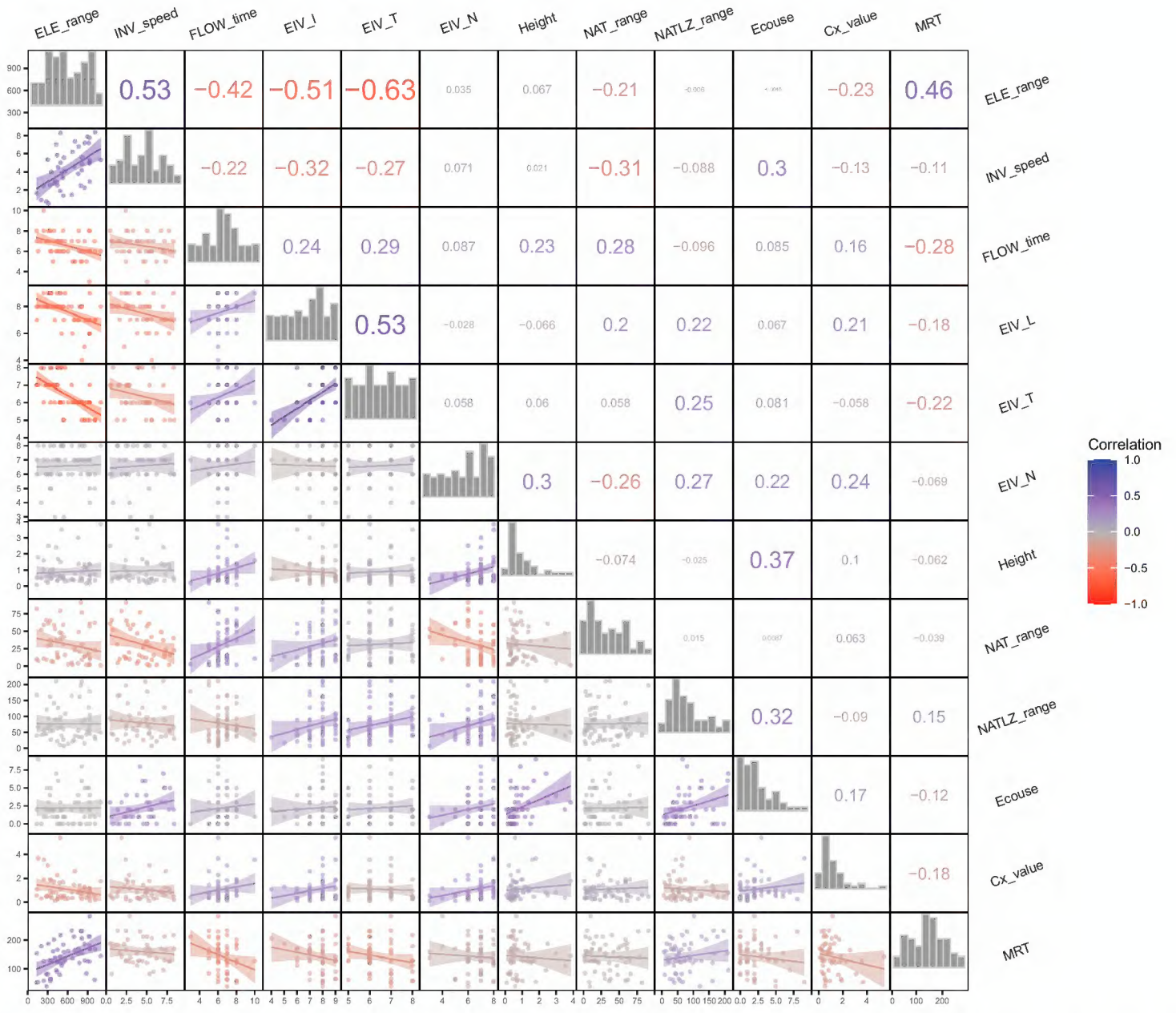

Figure A1. Pearson's correlation for all continuous variables collected in the study. ElE_range, elevation range; INV_speed, invasion speed; FLOW_time, flowering time; EIV_L, Ellenberg indicator values of light; EIV_T, Ellenberg indicator values of temperature; EIV_N, Ellenberg indicator values of nutrients; NAT_range, native range; NATLZ_range, naturalized range; Ecouse, economic use sum; Cx_value, monoploid genome size; MRT, minimum residence time.

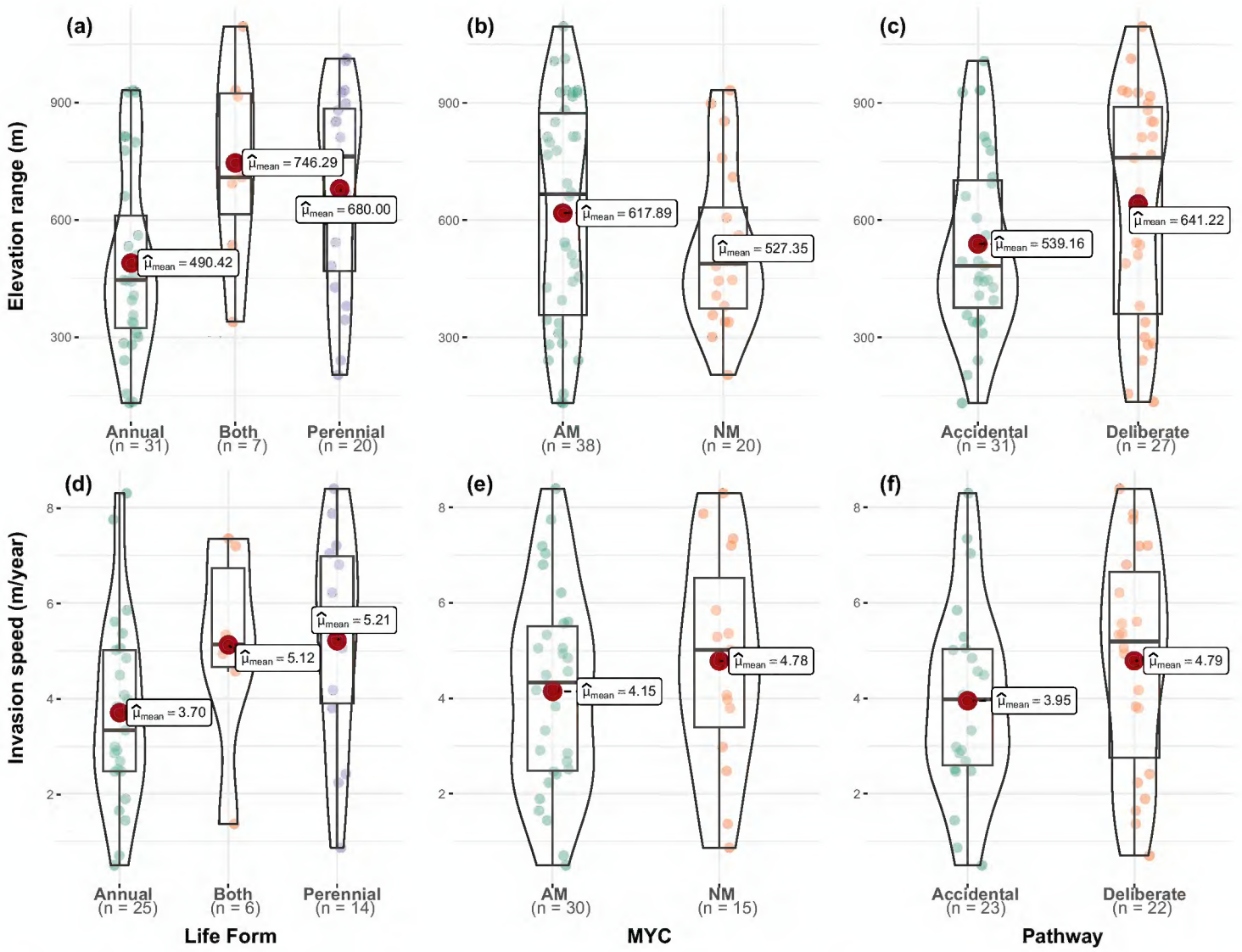

Figure A2. Violin plots of the elevation ranges and invasion speeds for the 58 alien species considering their life spans, mycorrhizal types, and introduction pathways. For the boxplots inside each violin plot, the horizontal line represents the median, the red dot indicates the mean, and the box represents the interquartile range. *P*-values were calculated using phylogenetic ANOVA models, and none of them are significant.

Supplementary material 1

Data used for the analysis

Authors: Miao-Miao Zheng, Petr Pyšek, Kun Guo, Hasigerili, Wen-Yong Guo

Data type: csv

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